CANOPY GAP CHARACTERISTICS AND DROUGHT INFLUENCES IN OAK FORESTS OF THE COWEETA BASIN[1]

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Abstract.   Canopy gaps in southern Appalachian mixed-*Quercus* forests were characterized to assess the impact of the 1985–1988 record drought on patterns of tree mortality in relation to topographic variables and changes in overstory composition. Using permanent transects, we sampled 68 canopy gaps within the Coweeta Basin. Among 1–5 yr old gaps, the most common gap type was the 1-yr-old single-tree snag, accounting for 49% of all gaps sampled; 65% of all gaps occurred within 2 yr of the drought peak. Gap area ranged from 40 to 850 m², averaged 239 m², with a median of 152 m². Analysis of 1988 color infrared (IR) aerial imagery yielded a gap formation rate of 0.8 gaps·ha⁻¹·yr⁻¹ in mixed-*Quercus* stands affecting 2.0% of the area in this forest type in 1988. The most frequent gap-forming species were *Quercus coccinea, Q. rubra,* and *Q. velutina,* respectively. Evidence suggests that moisture stress brought on by severe drought increases the susceptibility of *Quercus* species to the shoe-string fungus *Armillaria mellea,* which may result in significant shifts in canopy composition in these forests.

Key words: canopy gaps; Coweeta; disturbance; drought; mixed-oak forests; predisposal; southern Appalachians; tree mortality.

INTRODUCTION

Forest decline, in the context of Manion's (1981) "decline–disease theory," is thought to result from successively operating sources of stress (Hain 1987) that synergistically weaken trees in a given forest area. This phenomenon has been reported from most regions of the world, particularly from industrialized nations (Mueller-Dombois 1987). Common to all hypotheses of forest decline is the assumption that decline is a consequence of stress. Insects, fungal pathogens, air pollution, or lack of water and nutrients are thought to enhance risk of mortality by weakening trees' physiological resistance to further stress.

Severe drought is one agent of stress that has been shown to increase tree mortality. Hursh and Haasis (1931) related higher than normal mortality in red oaks to a severe drought that occurred in 1925. This drought has also been implicated in the reduction of subsequent growth rates of red oak species, primarily northern red oak (Tainter et al. 1984). In addition, subsequent high rates of red oak mortality following other drought events in the 1970s (Starkey et al. 1989) may in part reflect

effects of the earlier drought. Stringer et al. (1989) reported similar growth decline and increased mortality in the red oak group in an eastern Kentucky forest and hypothesized their relationship to the 1925 drought in combination with more recent periods of below-average rainfall.

Another study of oak decline in the southern USA conducted in the mid-1980s (Starkey et al. 1989) documented scarlet oak mortality from Arkansas to North Carolina. Shoe-string fungus (*Armillaria mellea* Vahl ex Fr.) frequently occurred in the declining and dead trees. This soil-borne fungus damages and kills the root systems only of trees previously stressed by severe drought (Wargo 1972, 1977) or other agents.

From late 1985 through 1988, lower and midelevation forests of the Coweeta Basin experienced the most severe drought on record in terms of duration and accumulated precipitation deficit. For this period, annual precipitation averaged 136 cm, 24% below normal. In 1986, the peak of the drought, annual precipitation was 124 cm, 31% below normal (USDA Forest Service, *unpublished data*). Using streamflow as a surrogate for precipitation, the return period for this drought has been estimated to be 233 yr, using a modified Z-T method of extreme value analysis for small watersheds (Swift et al. 1989). In comparison, the drought of 1925 produced a 44% precipitation deficit at Asheville, North Carolina (Hursh and Haasis 1931). Although the intensity of these droughts is similar in

magnitude, it is the combined effect of intensity and duration that better expresses the impact of such events.

We expected that the intense 1985–1988 drought would have major structural impacts upon the oak forests of the Coweeta Basin through differential species and site mortality patterns and a high incidence of canopy gap formation. The objectives of this study were to: (1) assess the impact of this recent drought on tree mortality rates; (2) examine characteristics of subsequent canopy gaps; and (3) examine the relationship of canopy gap formation to complex topographic moisture gradients.

Given the magnitude of this drought, the effects are likely long term as appeared to be the case with the drought of 1925. Furthermore, we hypothesized that old, large, relic trees that survived past disturbances such as fire and high-grade logging (pre-1930s) would be more susceptible to drought-induced mortality than younger individuals.

MATERIALS AND METHODS

Study site

This study was conducted in the 1626-ha Coweeta Basin (675–1592 m elevation), an experimental forest within the Coweeta Hydrologic Laboratory. The laboratory is administered by the USDA Forest Service and is a Long-Term Ecological Research (LTER) site (Swank and Crossley 1988). It is located in the Blue Ridge physiographic province of the southern Appalachians (latitude 35°03′ N, longitude 83°25′ W) near Franklin, North Carolina. Mean annual precipitation ranges from 178 cm (low elevations) to >250 cm (high elevations) with <5% falling as snow in the lower elevations. Precipitation is usually evenly distributed throughout the year. Mean annual temperature is ≈13°C (Swift et al. 1988). The soils are primarily Ultisols (Typic and Humic Hapludults) and Inceptisols (Umbric and Typic Dystrochrepts, and Typic Haplumbrepts; Velbel 1988).

The mixed-oak forest type (Day et al. 1988) is widely distributed over the basin, and provided the primary sampling sites in this study. The most widespread and important canopy species in this forest type is chestnut oak (*Quercus prinus*), which is most frequent at midelevations. Northern red oak (*Q. rubra*) may dominate at the high elevations, while at low elevations, white oak (*Q. alba*) and black oak (*Q. velutina*) are important. Scarlet oak (*Q. coccinea*) dominates the xeric mixed-oak type as well as oak–pine forests on drier slopes and ridges at low- and midelevations (canopy dominants are listed in Table 3). All species nomenclature follows Little (1979).

Gap sampling

In 1988 we walked nine permanent parallel Forest Service vegetation transects and systematically sampled canopy gaps located entirely or partially within these transects on midelevation slopes and ridges in mixed-oak forests. The transects are spaced at 201-m intervals along bearings of ≈N30° W and are 20.1 m wide. Within the transects are contiguous vegetation plots (20.1 × 40.2 m; 0.081 ha) that were initially established and inventoried in 1934 to provide baseline vegetation data for the Coweeta Basin (Day et al. 1988).

Cove and oak–pine forests were excluded from this study. Drought impacts under the very mesic conditions of cove forests were perceived to be minimal (B. D. Clinton, *personal observation*). Gaps created by pitch pine (*Pinus rigida*) were excluded because of their unique nature (Smith 1991): most are very large multiple-tree gaps and typically result from southern pine beetle infestation (*Dendroctonus frontalis* Zimmerman; Kuykendall 1978). In addition, mortality of individual pitch pines, typically attributable to suppression, does not create significant canopy openings.

In this study, canopy gaps were characterized based on the "expanded gap" definition (e.g., gap boundary defined by the base of surrounding canopy trees; Runkle 1981). Border trees whose crowns were a component of the upper canopy defined the gap boundaries. The criteria for sampling gaps in the transects were (1) a portion of the "expanded gap" overlapped the permanent transect and (2) the gap had formed within 5 yr of sampling. We recognize the risk for certain sampling biases related to the transect method (Barden 1989). It was difficult at times to determine the exact plot boundary intersection with the gap due to the presence of dense evergreen understory. Regarding the second criterion, beyond 5 yr it is difficult to identify the species responsible for the gap due to the degree of decomposition and resultant bark deterioration (Harmon 1982). In addition, older gaps (>5 yr old) are more difficult to age accurately. However, 5 yr is not a sufficient length of time for canopy gaps to become unrecognizable in these forests, even for single-tree gaps and, hence, 5-yr-old gaps were easily identifiable. Furthermore, gap boundaries were defined by the base of the surrounding canopy trees; therefore, estimates of gap area were not affected by gap closure phenomena. This is consistent with estimates of rates of gap closure (5 and 12% yr⁻¹) and gap longevity (8–20 yr) reported for southern Appalachian forests (Barden 1989). In addition, Frelich and Martin (1988) reported that sugar maple (*Acer saccharum*) gap trees would take 6–35 yr to reach the surrounding canopy in northern hardwood forests.

Gap and site characteristics

The measurement techniques were modified from those of Runkle (1982). Gaps were classified into four types based on the mechanism of formation (Table 1). A distinction was made between windthrown trees (i.e., ones that create pits and mounds) and basal-shear trees (i.e., trees that were snapped off above ground). Gap

age was inferred to the nearest year based on lengths and numbers of internodes on previously suppressed individuals growing within the area of impact. The formation of the oldest, substantially longer internodes were assumed to be coincident with gap formation. Species such as red maple (*Acer rubrum*) and Fraser magnolia (*Magnolia fraseri*) responded quickly and reliably to the change in environment, developing longer branch internodes following gap formation. The makers of the youngest gaps had intact twigs with buds, and were presumed to have died during the winter of 1987–1988; they were assigned to 1988 as the year of gap formation.

Trees responsible for canopy gap formation were identified to species from bark and wood, and diameter at breast height (dbh) was measured to the nearest 0.1 cm with a diameter tape at 1.4 m above the soil surface. In older gaps, care was taken to insure that outside diameter was measured on stems where the bark had slipped or had deteriorated at breast height. Diameter was converted to basal area (in square metres). In multiple-tree gaps, it was difficult to determine which tree, if any, initiated the opening. Hence, for those gaps basal area of all potential gap makers was summed. The age of gap-forming trees was estimated through the use of age vs. dbh regression equations developed by Iglich (1975) and Spring (1973) for the species at Coweeta.

Gap area was estimated as for an ellipse, based on the two longest perpendicular axes in the gap. Most gaps were at least roughly elliptical.

The topographic characteristics of each canopy gap (aspect, elevation, slope configuration, slope position, and percent slope) were measured. Aspect was measured to the nearest of 16 cardinal points with a compass. It was converted to a relative moisture index, with SSW being the most xeric and NNE the most mesic, based on work at Coweeta by Day and Monk (1974):

NNE 16, NE 15, N 14, ENE 13, NNW 12, E 11, NW 10, ESE 9, WNW 8, SE 7, W 6, SSE 5, WSW 4, S 3, SW 2, SSW 1.

In addition, for each gap a Topographic Relative Moisture Index (TRMI; modified from Parker 1982) was determined from aspect, slope configuration, percent slope, and slope position. Values for slope position, aspect, and slope steepness were derived from Parker (1982). We added an ordinal measure of slope configuration (concave = −1, flat = 0, convex = +1) for both the upslope and across-slope profiles for each gap. These six values were then summed to determine the TRMI.

Elevation was obtained from a 15.2-m contour interval topographic map. Ridge, upper slope, midslope, and lower slope positions were determined visually on site for each gap. Slope was measured in percentages by averaging two measures of slope taken on opposite sides of the gap makers with the use of an Abney level.

Canopy gaps (snags) were also sampled from 1988 color infrared aerial imagery (1:8000; 5 m resolution) to obtain an estimate of gap formation for the entire mixed-oak forest type in the basin. Area control was accomplished by sampling within known untreated unit watersheds and ungauged areas that could be easily delineated on a topographic map. The area sampled was evenly divided between north and south aspects and stratified within watersheds with respect to major forest types. Care was taken to distinguish declining individuals (trees showing crown die-back) from dead ones. Only gaps with conclusively dead crowns were tallied. Gap formation rates (gaps per hectare per year) were based on distributions of gap area, type, and age as determined from our transect survey of gaps and were calculated with the following formula:

$$\text{gap formation rate} = \frac{G_D \times G_A}{10\,000} \Big/ T,$$

where G_D = gap density (number per hectare) detected on aerial image, G_A = mean gap area (in square metres) as determined from ground sampling, T = 5-yr sampling period for this study. Approximately 20% of the snags identified on the photos were age and area verified on the ground to validate the assumption that the distributions of gap age and area were similar to that determined in the more accurate field survey of gaps.

Statistical analysis

We hypothesized that drought effects would not become significant until the year following the drought peak. Discriminant analysis (SAS 1987) was used to develop a linear classification function for testing how well variables discriminated between gaps occurring immediately following the peak of the drought (Group 1; 1987 and 1988) from those that occurred during and before the drought peak (Group 2; 1984–1986). Variables were percent slope, slope position, elevation, basal area of the maker, slope configuration, TRMI, aspect, and gap area. Stepwise discriminant analysis (Sullivan 1981) was used to identify significant models based on these variables. The assumption of equal covariance matrices among groups was made and prior probabilities were assigned proportionally (Group 1 = 0.66, Group 2 = 0.34) (Sullivan 1981). Posterior probabilities of misclassification were computed for each observation as a method for estimating percent misclassification.

A folded-form F statistic was used to test for homogeneity of variances (SAS 1987). When variances were equal, parametric tests were used to examine differences among means for the gap characteristic variables. When variances were not homogeneous, an appropriate t test and Satterthwaite's approximation for computing degrees of freedom were used (SAS 1987). Duncan's multiple-range test was used to make simultaneous comparisons of variable means where

TABLE 1. Distribution of sampled gaps ($n = 68$) with respect to mode of formation. Median gap area for all gaps = 152 m². Means with the same letter do not differ significantly at the .05 level (Duncan's multiple-range test). The term "snag" is used to mean a standing-dead individual tree on the landscape.

Type	Mode of formation	Gap area (m²)		
		Mean	SE	% of gaps
1	Single-tree snag	172[b]	24.33	50
2	Multiple-tree snag	338[ab]	50.63	24
3	Windthrow (pits and mounds)	201[b]	41.86	4
4	Basal-shear fall	398[a]	82.33	7
Others	Complex of major types	217[ab]	53.95	15
	Totals	239		100

parametric tests were appropriate. A chi-square (χ^2) test of independence was conducted on a contingency table of gap frequencies by age class and position ($\alpha = .05$) as a means of testing for gap age–slope position interaction.

RESULTS

Gap types and characteristics

Of the canopy gaps in these midelevational mixed-oak forests, 74% were standing-dead types (Table 1). Over 70% of single-tree standing-dead snags were created in the 2 yr following the 1986 drought peak. In addition, 66% of all gaps (total of all four types) were created after 1986. Gap age distributions for single-, multiple-tree, and all others combined are presented in Fig. 1.

For single-tree snags ($n = 34$), the only characteristic significantly correlated with gap area was basal area of the gap maker ($r = 0.39$; $P = .01$). For multiple-tree snags ($n = 16$), basal area of the gap maker was significantly correlated with TRMI ($r = 0.39$; $P = .04$), with slope ($r = -0.49$; $P = .01$) and with gap area (r

= 0.89; $P = .0001$). For all gaps combined, gap area was found to be negatively correlated with slope ($r = -0.55$; $P = .003$; $n = 68$). Slope did not differ between single- and multiple-tree snags. For all gaps ($n = 68$), basal area of the gap maker was significantly correlated with elevation ($r = 0.35$; $P = .004$), TRMI ($r = 0.23$; $P = .05$), and slope ($r = -0.33$; $P = .006$).

Topographic position was not related to the timing of gap formation (Table 2). More of the detected gaps had formed in 1988 (41%) than in any other year. Overall, gaps were fairly evenly distributed among the three slope positions (Table 2). Nearly 40% of all gaps sampled had formed on northern aspects and 34% had formed on the more mesic sites (lower slopes). Of the gaps sampled, 67% occurred on ridge and midslope positions.

Gap area ranged widely, but most gaps were <200 m² (Fig. 2). Gap area was significantly correlated with basal area of the gap maker ($r = 0.70$; $P = .0001$; $n = 68$) and with slope ($r = -0.28$; $P = .02$; $n = 68$). The multiple-tree gaps had the greatest mean area (Table 1); however, the largest gap sampled (825 m²) was a single-tree snag.
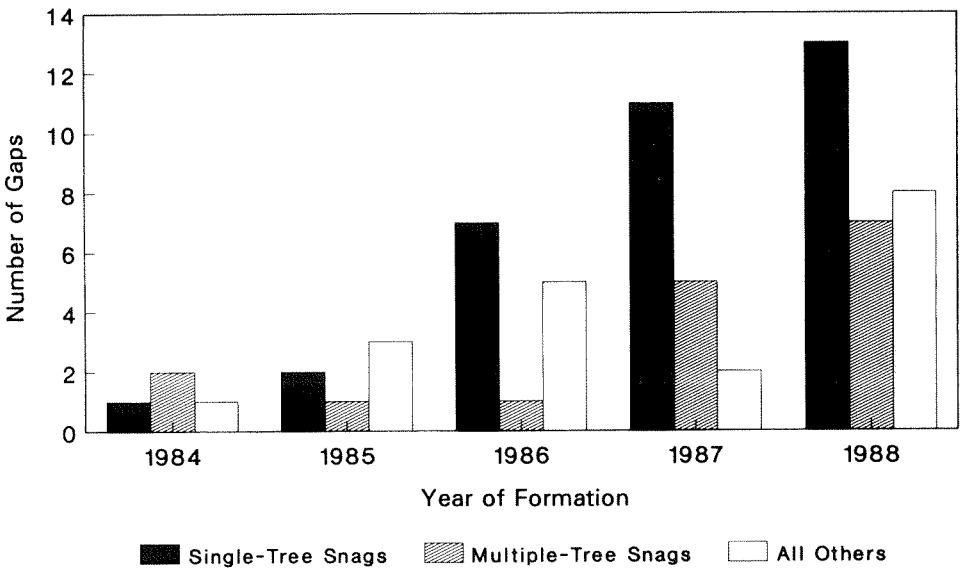

FIG. 1. Relation of gap types (mode of formation; see Table 1) to year of formation.

TABLE 2. The distribution of canopy gaps with respect to slope position and age class (year of formation: 1 = 1988, 2 = 1987, 3 = 1984–1986). Cell values represent proportions of total number of gaps in each age/position category.*

Gap age	Slope position			
	Ridge	Middle	Lower	Totals
1	13.2 [9]	16.2 [11]	11.8 [8]	41.2 [28]
2	4.4 [3]	10.3 [7]	10.3 [7]	25.0 [17]
3	5.9 [4]	16.2 [11]	11.7 [8]	33.8 [23]
Totals	23.5 [16]	42.7 [29]	33.8 [23]	100 [68]

* A chi-square (χ^2) test of independence was conducted on a 3 (age classes) by 3 (slope positions) contingency table of frequencies (Pearson χ^2 = 2.235, P = .693, df = 4). Sample size is indicated in brackets.

Gap-forming species

Of the canopy gaps sampled in this study (n = 68) 83% were created by oak species (Table 3). Most of the gap makers ranged in size from 30 to 60 cm dbh (Fig. 2). However, the dominance of scarlet oak is primarily responsible for the shape of this distribution. The other three species in Fig. 3 approximate a bell-shaped distribution peaking around 50–55 cm.

Scarlet oak created 44% of all single-tree snags and contributed to nearly 60% of all gaps sampled. Based on age–dbh models developed from the same population of scarlet oaks at Coweeta (Spring 1973, Iglich 1975), gap makers in this species were predicted to be from ≈150 to 200 yr old. Black oak had the largest average dbh of all the dominant gap makers. The average dbh for this species was 49.6 cm compared to

TABLE 3. Species responsible for canopy gap formation in the midelevation mixed-oak forests at Coweeta. Included are relative contributions to gap formation by species and background data on percent stand density occupied by gap maker species, based on 1970 survey of permanent plots at Coweeta (density based on stems ≥ 15 cm dbh).

Gap maker species	% of total gaps	% stand density
Scarlet oak (*Quercus coccinea*)	44	6
Northern red oak (*Q. rubra*)	16	6
Black oak (*Q. velutina*)	11	8
Hickory spp. (*Carya*)	11	8
Chestnut oak (*Q. prinus*)	7	10
American basswood (*Tilia americana*)	5	<1
White oak (*Q. alba*)	4	5
Fraser magnolia (*Magnolia fraseri*)	2	<1
Totals	100	<44

47.4 cm for northern red oak and 37.8 cm for scarlet oak. However, these means are not significantly different as determined by Duncan's multiple-range test (SAS 1987).

Distribution and rates of gap formation

Analysis of infrared aerial photographs yielded a frequency of 1.7 gaps/ha in mixed-oak forests. In comparison, an estimated 2.3 gaps/ha occurred in our ground sample. On the photos, the frequency of gaps in lower and upper coves, defined as the mesic mixed cove–hardwood forest type, was much lower (0.7 gaps/ha).

Standing-dead snags formed during 1984–1988 occupied ≈4% of the area of mixed-oak forests (1.7 gaps/ha × 225 m^2 mean area for transect-measured standing-dead snags) as determined from aerial photo sam-
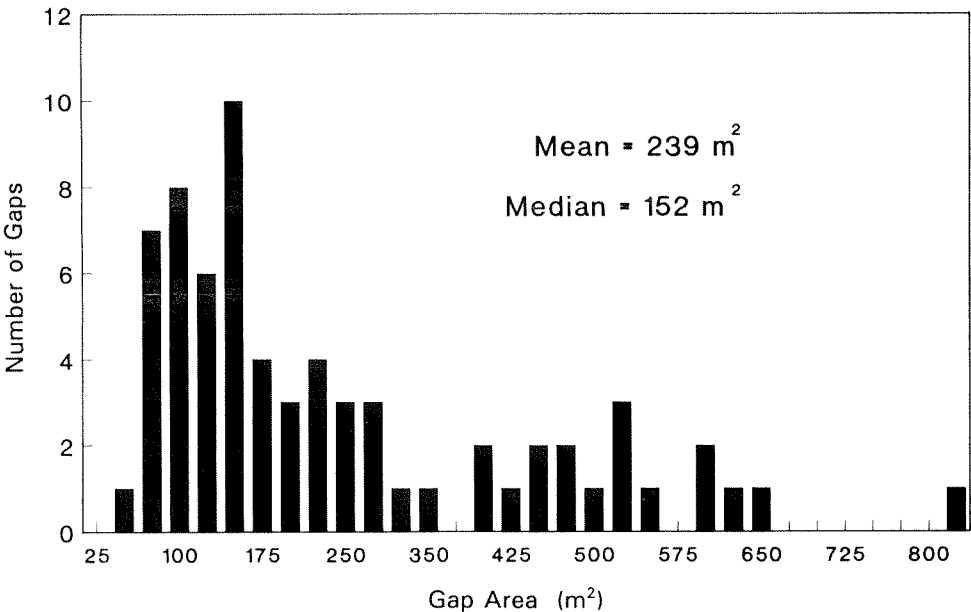

FIG. 2. Distribution of canopy gap area in square metres. X axis indicates the upper limit of each size class.
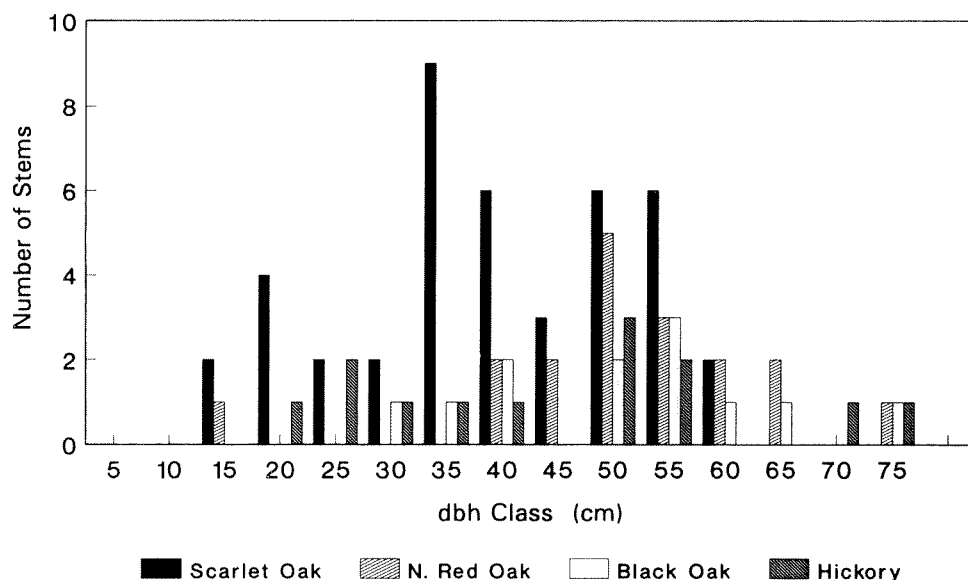
FIG. 3. Diameter distribution (5 cm diameter classes) of the four species most frequently observed as gap makers.

pling. Using the age class distribution determined from transect-measured gaps, an estimated 70% of the gaps identified on the aerial photos formed after 1986 ($\approx 3.0\%$ of the mixed-oak forest area). Furthermore, 2.0% of the land area was affected in 1988 alone. Making the assumption of equal rates of canopy gap formation (Romme and Martin 1982), we can compare average rates of gap formation for the 2 yr prior to the peak of the drought (1984–1985) with the following 2 yr (1987–1988). At 1984–1985 rates, complete canopy turnover in the basin's mixed-oak forests would require 526 yr; at 1987–1988 rates, turnover would require 66 yr.

Discriminant analysis (see *Methods* for list of variables) failed to discriminate between the two age classes of gaps (Wilks' lambda = 0.85; F = 0.96; P = .49). While only 30% of the original observations were misclassified, the classifier had difficulty discriminating between the two age groups of gaps. Only 11% of the Group 1 (post-1986) observations were misclassified, but 65% of the Group 2 (before and during 1986) observations were misclassified. Therefore, using drought as a point event, there appears to be little difference between the means of the topographic variables and gap characteristics for the two groups.

Few of the measured characteristics of post-1986 gaps (see *Methods*) differed significantly from those of gaps formed before or during 1986 (t test). Means differed only for gap area (1987–1988 = 219 m², pre-1987 = 279 m²; P = .03; n = 68) and for basal area of gap maker (1987–1988 = 0.22 m², pre-1987 = 0.31 m²; P = .01; n = 68). Simple linear regression was used to relate gap area and basal area for all gaps combined:

$$\text{Gap area} = 65.88 + 685.1 \cdot \text{BA};$$
$$r = 0.70; P = .0001,$$

where BA = basal area (in square metres) of the gap

maker (summed for multiple-tree gaps). Gap area for all single-tree snags alone was also significantly correlated with basal area (r = 0.39) as were all multiple-tree snags (r = 0.89).

DISCUSSION

Characterization of canopy gaps

Most canopy gaps in this study were standing-dead snag types (Table 1). Wind-induced gaps (windthrow and basal shear types; Table 1) accounted for only 11% of all gaps sampled. This disproportionate number of standing-dead snags, consistent with a canopy-level drought response in these oak forests, differs from findings of many gap studies in the southern Appalachians where wind-induced gaps predominated (Barden 1979, 1981, Runkle 1981, 1982, Romme and Martin 1982, White et al. 1985). These earlier studies were commonly conducted in old-growth cove forests in which tree mortality processes and tree replacement patterns are likely very different (Barden 1980). Thus in southern Appalachian second- and third-generation mixed-oak stands, standing-dead snags appear to be an important phenomenon influencing tree replacement patterns.

Mean gap area (239 m²) was strongly influenced by the larger, multiple-tree gaps formed prior to the drought year. Mean area for all gaps is an overestimate for postdrought gaps, which were primarily of the single-tree variety (172 m²). Gap area had a significant negative correlation with percent slope (r = -0.55; P = .003) and positive correlation with basal area of the gap maker for all gaps (r = 0.70; P = .05). Furthermore, basal area of the gapmaker was significantly negatively correlated with percent slope (r = -0.33; P = .006). Together, these relationships imply the existence of a

site quality gradient within the sampling area (i.e., the steeper the slope, the smaller the individual, the smaller the gap).

Significant differences between pre- and postdrought gaps existed for basal area of the gap maker(s), only. Our oldest gaps were primarily multiple-tree types and fell in the "before drought" category. Consequently, these gaps had a strong influence over the outcome of the analysis. However, the average basal area per stem for all multiple-tree gaps was 35% less than stems of single-tree snags, which supports the hypothesis that most of the individuals affected by the drought were large older trees that were more susceptible to agents of stress.

Differential species mortality

Gap makers were primarily species of the red oak group, dominated overall by scarlet oak (Table 3). An oak decline study in the southern USA (Starkey et al. 1989) also found scarlet oak to be the most frequently dead or declining species, primarily linked to a drought-induced outbreak of *Armillaria mellea.* This is consistent with our findings along with visual confirmation of the widespread abundance of this fungus at Coweeta (D. J. Lodge, *personal communication*).

Research by Tainter et al. (1984) related mortality in northern red oak to climatic variables where growth rate declines began 60 yr earlier as a consequence of the severe drought of 1924–1925. In that study, recovery was never fully achieved and high rates of mortality were observed during less intense drought events in the 1970s. Their study implicates water stress as a major contributor of predisposition to secondary pathogen effects, and that subsequent mortality may take years or decades to become fully manifested. Hence, severe drought could be viewed as a "set point" in the life histories of some individuals. At this time trees become predisposed to mortality due to their loss of ability to compete for limited resources or to combat secondary pathogen related stress.

Trees become less efficient at transporting water, nutrients, and photosynthate with increasing age and size (Spurr and Barnes 1973, Tomlinson and Zimmerman 1978). The greater aboveground biomass must be supported by proportionally less photosynthetic tissue (Harper 1977). Given that the average ages of the gap makers in our study were ≈150–200 yr old, their presumed inability to physiologically respond to moisture stress may have predisposed them to higher rates of mortality than younger trees.

Drought as a disturbance regime

Based on relative gap frequencies measured in this study, response at Coweeta to the 1986 drought was more severe in the midelevational mixed-oak forests, which dominate much of the southern Appalachians, than in cove forests. The oak decline and mortality observed over much of the southern states from Ar-

kansas to Virginia during the same time period (Starkey et al. 1989) suggests that this particular event had regional consequences. Given our results and the work of others (Tainter et al. 1984, Stringer et al. 1989), there is a strong likelihood that this regional response to disturbance was initiated by drought.

The recent drought-related pulse of mortality may have longer term impacts upon stand structure and function throughout the southern Appalachians. The mode of disturbance (i.e., standing-dead snags) implies that important classes of microhabitats are not produced. Species such as pitch pine that require more extreme site alteration (Barden and Woods 1976), commonly associated with wind-induced tree mortality, are at a distinct disadvantage compared to those that do not and rely primarily upon advance sapling regeneration strategies. In addition, the lack of a pulse addition of coarse woody debris, typical of wind-induced gap formation, may reduce regeneration opportunities for species such as sweet birch (*Betula lenta*) and eastern hemlock (*Tsuga canadensis*), whose reproductive strategies include "nurse logs" as fresh substrate for seed germination (Fowells 1965). This is not to say that other important classes of microhabitats are not produced. The standing-dead tree and the shade it casts are important microhabitats for many organisms and processes. Thus, effects of standing-dead snags may have important influences on micro- as well as macro-level processes.

We must also begin to assess ecosystem-level impacts of such climatic alteration of forest structure. Canopy openings and shifts in species composition alter microclimatic factors such as light, temperature, and moisture, which regulate nutrient cycling processes. For example, the response of the nitrogen-fixing black locust (*Robinia pseudo-acacia*) in large gaps and shifts in litter quality or decomposition rates of leaves of different species are two potential manifestations. The long-term importance of increasing our understanding of acute and chronic drought impacts upon forest structure and function is central to anticipating the full impacts of predicted long-term climatic change.

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